TEMPERATE FLORAS: THE NORTH PACIFIC CONNECTION

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ABSTRACT

The affinities between the floras of eastern Asia and eastern North America are widely recognized, but close affinities also exist between some elements of the floras of northeastern Asia (China, eastern USSR, and Japan) and northwestern North America. This relationship is indicated in taxonomic treatments either by no formal taxonomic recognition of the disjunct populations, or by varietal or specific separation of the disjuncts. After listing 31 examples of this disjunction, I offer a protocol for their comparative, evolutionary study. In addition to making careful morphological and cytological comparisons, it should be possible to test the degree of genetic similarity and ecological comparability of the vicariants. By growing them for use in breeding tests, allozyme studies, and for controlled environment testing, it should be possible to determine the degree of genetic similarity or divergence that the vicariants may reveal. By comparing physical and biotic aspects of their ecologies, one could assess their habitat/niche similarities. Data from such studies can test either of two hypotheses: (1) The disjuncts are conservative and have not diverged in any significant way since their separation. (2) The disjuncts have diverged to become passively genetically isolated *and* ecophysiologically distinct, despite their close taxonomic affinity. At present, only very few examples of paired genetic-ecologic tests are known.

Over the years—and at this present symposium—botanists and biogeographers have emphasized the connections between the floras of eastern Asia and those of eastern North America. From Linnaeus, Frederick Pursh, and Asa Gray to contemporary phytogeographers (Graham, 1972; Li, 1952, 1972), the causes and consequences of the floristic connections between the two continents' eastern areas have occupied the geobotanical stage. Yet a few botanists have noted the substantial affinities between temperate eastern Asia and the northwestern Pacific side of North America. Papers by Hara (1952, 1956) and Mizushima (1972) remind us that the North Pacific rim from Japan and mainland China to the American Pacific Northwest provides a large number of floristic links between the oriental Old World and the western New World.

It has been remarked (Mizushima, 1972) that the North Pacific connection has been overlooked probably because the contemporary floras are in the main so different. Through the early to mid Tertiary, a nearly continuous mixed mesophytic forest maintained the floristic similarities between eastern Asia and much of temperate North America. Then, climatic changes, no doubt ushered in by massive orogenies in the Pacific Northwest, largely obliterated the mixed mesophytic forest type in the Pacific Northwest (Graham, 1972).

What affinities remain, though, are substantial and suggest that some taxa survived the erasures of much of that flora of the late Tertiary. Or, perhaps, the Pacific Northwest in the late Tertiary developed floristic elements that spread from east to west—up the coast of western North America and down the east coast of Asia. Could, for example, vicariants in *Lysichitum* and *Rubus* have arrived in eastern Asia in a counter-clockwise migration? Further, it is probable that the number of vicariants and disjunctions in the North Pacific floras might have diminished further during the Pleistocene. So, we have a set of biogeographic conundrums for many plant distributions along the North Pacific rim. Questions that these bicontinental distributions pose to the student of evolution are also genetic ones. How much genetic "distance" separates the vicariants? Have the vicariants become reproductively isolated in the passive, allopatric mode, or are some still inter-fertile?

This paper first reviews some of the examples of the North Pacific floristic connection and then proposes ways to test the degree of genetic divergence between vicariant taxa.

EXAMPLES OF EASTERN ASIA–WESTERN NORTH AMERICA FLORISTIC AFFINITIES

Vascular plants with amphi-Pacific affinities can be categorized in three modes: taxonomic, geographic, and ecological. Furthermore, these

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TABLE 1. Some taxa of eastern Asian–western North American affinities.

Eastern Asia	Western North America	Range	Continuity	Habitat	Taxonomic Status
Woodwardia orientalis Sw.	*W. fimbriata* J. E. Smith	Japan & Washington	Discontin.	Mesic coastal to montane	Vicar. spp.
Cryptogramma crispa (L.) R. Br.	*C. crispa*	Circumboreal	Discontin.?	Mesic-xeric, coastal/montane	Conspecific
Pinus thunbergii Parl.–*P. densiflora* Sieb. & Zucc.	*P. contorta* Loud.	Circumboreal	Discontin.	Mesic-xeric, coastal/montane	Vicar. spp.
Calamagrostis purpurascens R. Br.	*C. purpurascens*	Eastern Asia + western North America	Contin.?	Mesic-xeric, coastal/montane	Conspecific
Deschampsia atropurpurea (Wahl.) Scheele	*D. atropurpurea*	Cosmopolitan	Contin.	Mesic, montane	Conspecific
Lysichitum camtschatcense Schott	*L. americanum* Hultén & St. John	Japan to California	Discontin.	Mesic	Vicar. spp.
Fritillaria camschatcensis Ker	*F. camschatcensis*	Japan to Washington	Contin.?	Mesic, coastal	Conspecific
Maianthemum dilatatum Nels. & MacBr.	*M. dilatatum*	Japan to western North America	Contin.?	Mesic	Conspecific
Platanthera chorisiana Rchb. f.	*P. chorisiana*	Japan to Washington	Contin.	Mesic	Conspecific
Alnus crispa Ait.	*A. crispa* var. *sinuata* Regel	Eastern Asia–western North America	Contin.	Mesic, montane	Vicar. vars.
Coptis japonica Mak.	*C. aspleniifolia* Salisb.	Japan–Southern British Columbia	Discontin.?	Mesic	Vicar. spp.
Achlys triphylla DC. var. *japonica* (Max.) Fukuda	*A. triphylla* var. *triphylla*	Japan to California	Discontin.	Mesic	Vicar. vars.
Saxifraga bronchialis L. ssp. *funstonii* (Small) Hult.	*S. bronchialis* ssp. *austromontana* Pip.	Siberia–North America (circumbor.)	Discontin.	Montane	Vicar. vars.
Geum calthifolium Smith var. *nipponicum* Hara	*G. calthifolium*	Japan to British Columbia	Contin.?	Mesic, coastal	Vicar. vars.
Rubus pedatus J. E. Smith	*R. pedatus*	Japan to southern Oregon	Discontin.?	Mesic-montane	Conspecific
R. vernus Focke	*R. spectabilis* Pursh	Japan to NW California	Discontin.?	Mesic	Vicar. spp.

TABLE 1. (Continued).

Eastern Asia	Western North America	Range	Continuity	Habitat	Taxonomic Status
Spiraea betulifolia Pallas ssp. *aemiliana* Hara	*S. betulifolia* ssp. *lucida* (Dougl.) Hitch.	Circumboreal?	Contin.?	Mesic-xeric	Vicar. spp.
Oplopanax horridum (Smith) Miq. var. *japonicum* Hara	*O. horridum*	Eastern Asia–western & central North America	Discontin.	Mesic	Vicar. vars.
Acer japonicum Thunb.	*A. circinatum* Pursh	Japan–Northern California	Discontin.	Mesic, coastal	Vicar. spp.
Cassiope stelleriana (Pall.) DC.	*C. stelleriana*	Eastern Asia to Washington	Contin.?	Mesic-montane	Conspecific
Menziesia pentandra Maxim.	*M. ferruginea* Smith	Japan–Oregon	Discontin.	Mesic-coastal	Vicar. spp.
Rhododendron kamtschaticum Pall.	*R. kamtschaticum*	Japan to Alaska	Contin.?	Polar/boreal	Conspecific
Fauria crista-galli Makino ssp. *japonicum* Gillett	*F. crista-galli*	Japan to Washington	Contin.?	Mesic-coastal	Vicar. vars.
Boschniakia rossica Fedtsch.	*B. rossica*	Eastern Asia–Alaska	Contin.?	Mesic-coastal	Conspecific
B. rossica	*B. hookeri* Walpers	Eastern Asia–Washington	Contin.?	Mesic-coastal	Vicar. spp.
Galium kamtschaticum Stell. var. *acutifolium* Hara	*G. kamtschaticum* var. *oreganum* Piper (= *G. oreganum*)	Eastern Asia–Oregon	Contin.?	Mesic-coastal	Vicar. vars.
Valeriana sambucifolia Mikan var. *fauriei* Hara	*V. sitchensis* Bong.	Eastern Asia–California	Discontin.	Mesic-montane	Vicar. spp.
Campanula lasiocarpa Cham.	*C. lasiocarpa*	Japan–Washington	Contin.?	Montane	Conspecific
Artemisia arctica Less. ssp. *arctica*	*A. arctica* ssp. *arctica*	Japan–western North America	Contin.?	Boreal/montane	Conspecific
Achillea sibirica Ledeb.	*A. sibirica*	Japan–British Columbia	Contin.?	Montane?	Conspecific
Erigeron thunbergii A. Gray	*E. glaucus* Ker	Japan–California	Discontin.	Coastal	Vicar. spp.

categories are best viewed as elements of overlapping, multidimensional matrices. For example, some are strictly amphi-Pacific plants [*Achlys triphylla* (Smith) DC.] that are conspecific throughout their North Pacific distributions; others are circumboreal [*Cryptogramma crispa* (L.) R. Br.] or circumpolar [*Phippsia algida* (Sol.) R. Br.]. Some taxa are differentiated into varieties/subspecies or species along the North Pacific rim. Others are indistinguishable taxonomically. Some north Pacific taxa reach the full extent of the distributional arc, from Japan or adjacent mainland Asia, more or less continuously to the southern limit of the Pacific Northwest in northern California; others go only part of the way—for example, from Japan to the Aleutians or to Alaska. These are but some of the permutations of the amphi-Pacific floristic theme. Table 1 samples some of the various types of amphi-Pacific continuity.

From Table 1 we can glean some inferences about amphi-Pacific distributions: most examples are herbaceous perennials with coastal, mesic ecologies; bog species are common; and, apart from circumboreal and circumpolar examples, the strictly circum-Pacific cases can range from eastern Asia to western North America more or less continuously while others reach North America discontinuously (only the Aleutians, Alaska, British Columbia, or Washington).

No one can be sure what these variant distribution patterns are trying to tell us. I suspect they are the combined result of obvious phenomena: (1) the capriciousness of dispersal/distribution, (2) specific physiological tolerance ranges, and (3) the influence of past glacial and orogenic events.

Some Geological History in the North Pacific Area

The time from the Paleocene to the present (ca. 75 million years) has spanned major geological and climatic changes. The major phenomena include change in coastlines (including the flux of epiric seas); sea floor spreading; episodes of orogeny, especially vulcanism; and Pleistocene glaciation (and interglacial/post-glacial ameliorations). Through this span of turbulent time, floras waxed and waned, but remnants of floras had to persist to give their present amphi-Pacific distribution.

The early Tertiary seemed to have provided the most continuous stretch of habitat for temperate taxa. The mixed mesophyte forests of those times did pervade the North Pacific land masses (Wolfe, 1969, 1972). And, by the Miocene, most of the major floristic elements of the North Pacific rim were in place. Climatic change and geologic upheaval intervened to disrupt the continuities in varying degrees—from extinctions to major disjunctions. The latest perturbations, the Pleistocene ice encroachments, were the most recent to have affected this fluid, transitory biota.

It is instructive to note that Li (1952) inferred a difference in age among the various vicariants between the New and Old worlds. He (Li, 1952: 373) pointed out that the western North American–eastern Asian group of plants is a different and more recent one than the eastern Asian–eastern North American group. Li bases this assertion on (1) the relatively continuous, rather than discontinuous distribution of the amphi-Pacific plants; (2) their coastal, cool temperate to arctic distribution; and (3) their predominant herbaceous life-form. Li's arguments remind us that the intercontinental migrations and confluences of taxa (and of floras?) have taken place repeatedly throughout the past, have taken different paths, and today are expressed in a range of discontinuities.

Genetic Affinities of Vicariants and Disjuncts

It is assumed that the plants that show eastern Asia–western North America similarities are closely monophyletic (conspecific to vicariant taxa). It then follows that each example should show some degree of genetic affinity. Morphological resemblance is, of course, the initial basis for inferring genetic similarity. Further testing of the inferences of relationship from morphology must rely on genetic methods. Attempts to cross vicariants is a necessary next step. Degree of crossability and interfertility can be valuable measures of affinity. Other tests of genetic affinity could include isozyme comparisons via gel electrophoresis and could eventually employ comparisons of DNAs of paired taxa. For now, we will consider the evidence from crossing tests.

Several alternative hypotheses regarding genetic affinity of amphi-Pacific taxa are testable: (1) vicariants or disjuncts are conservative and have not diverged in any significant way and are interfertile; (2) disjuncts and vicariants have diverged to become genetically incompatible (either low crossability or reduced interfertility) and thus are reproductively isolated. It is to be expected that each particular pair of taxa will validate one

or the other of these hypotheses. Besides genetic/reproductive isolation, another component of potential genetic difference is surely to be ecotypic differentiation of vicariants or disjuncts. From other genecological studies (e.g., Clausen & Hiesey, 1958; Clausen et al., 1940, 1948), one would predict that even conspecific taxa in Asia and western North America will possess detectable ecophysiological differences that are bound to be genetically fixed.

In what follows, I review some of the evidence from crossability studies as it bears on the issue of genetic affinity between bicontinental disjuncts. Not all the examples illustrate the western North American–eastern Asian theme of this paper; rather, they illustrate the more general notion of degrees of genetic relationship between congeneric taxa in different continents. Thus, cases involving pines and certain hardwoods (e.g., *Liriodendron*) relate to connections via the north Atlantic between the Old World and the New, rather than to the North Pacific connection.

Few or no deliberate crosses have been performed to test either reproductive isolation or the ecotypic differentiation hypotheses as they apply to Asian–North American taxa. However, some bits of evidence come to light from horticultural, forestry, and agronomic literature, as follows:

Conifers. Breeding tests by Wright (1955) with *Picea* species from North America and Asia range from successful crossability (*P. jezoensis* × *P. glauca*) to unsuccessful (*P. asperata* × *P. sitchensis*).

Examples from *Pinus* (Mirov, 1967) include the curious case of *P. lambertiana*. It does not hybridize naturally with any of its western North American congeners, yet it is successfully crossed with two eastern Asiatic pines, *P. koraiensis* and *P. armandii*, also of the soft pine (*Haploxylon*) affinity. Intentional crosses among some Diploxylon pines from eastern Asia and western North America have been reported as failures (Duffield, 1952).

Broad-leaved trees. The Palmatum group of maples (*Acer*) is largely Asiatic. The one western North American species, *A. circinatum*, fails to cross with either *A. palmatum* or *A. japonicum*, both of Japan (fide J. A. Witt, University of Washington Arboretum).

Parks et al. (1983), at this symposium, reported that crosses between *Liriodendron tulipifera* (eastern North America) and *L. chinensis* (Hupeh, China) yield viable F_2 seed. Isozyme and flavonoid comparisons, coupled with the crossing data, indicate that the two taxa ". . . have not diverged very far from a presumed common ancestor . . . ."

Other woody plants. Crosses within and between series (= sections, more or less) in *Rhododendron* are often successful, yielding progeny of varying fertilities. The well-known azalea hybrids of the Knaphill and Koster origins are crosses of *R. occidentale* (western North America) with eastern Asiatic species, especially *R. japonicum*. Crossability and fertility is mainly high in these crosses with subseries *Luteum*. Asiatic members of series *Ponticum* have been crossed successfully with our western North American, *R. macrophyllum*.

Herbaceous monocots. *Iris* hybridizers have included some eastern Asia–western North America crosses in their many attempts to improve *Iris* for horticulture. Four different types of crosses all have yielded sterile F_1 progeny (fide Jean Witt, Seattle): *Iris* section *Sibiricae* × *I. setosa* (North American), *I. sibirica* × *I.* section *Californicae* (the so-called "*cal-sib*" hybrids), *I. douglasiana* × *I. lactea* (central Asia to Korea), and *I. longipetala* (northern California) × *I. sibirica*.

Herbaceous dicots. Very few cases of intentional crossings between eastern Asian and western North American congeners were found. Given the very rich but diffuse literature on plant breeding, more cases will surely come to light.

Taylor's (1967) study of intentional crosses in *Aquilegia* includes the hybrid *A. flabellata* (Japan) × *A. flavescens* (western North America); the F_1 had 61% stainable pollen and normal meiosis.

The scanty record of intentional hybridization between eastern Asian and western North American taxa makes it fruitless to draw any conclusions. Only when a program of deliberate crossing is mounted, involving a whole range of amphi-Pacific plants, can we test the genetic bases of the "North Pacific Connection." Many of the plants of Table 1 would be ideal subjects for such genetic testing. Indeed, the fuller lists of Mizushima (1972) and Hara (1952, 1956) provide ample taxa for pioneering a genetic analysis of amphi-Pacific biogeographic connections.

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